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A BRIEF STATEMENT OF REASONS FOR SOME CHANGES IN THE TERMINOLOGY OF INSECT WING-VENATION

By George Zalessky.

(*Zoological Museum of Moscow State University.*)

While working in the field of palaeo-entomology and investigating wing-venation of fossil as well as of recent insects, I became rather dissatisfied with both the interpretation and terminology employed of late by most palaeo-entomologists. The latter had primarily been founded on the well-known researches of Comstock and Needham (1898–1899) and of Comstock alone (1918), but afterwards it was subjected to certain modifications in the light of Lameere's theories (1923). Dissatisfaction with certain universally accepted terms was caused by a number of contradictions and inconsistencies I happened to find in the mode of treating venation. Hence, even in my earliest works on palaeo-entomology I made some alterations in the main venational scheme (1932, 1933) and began to employ my own nomenclature rather than that commonly used (1934, 1937 and others). In the course of time I had to change even more sharply my ideas concerning the original principles of wing-venation, ceasing to attach any great importance to the position of veins at the top or bottom of the wing folds, *i.e.* to the discrimination between convex and concave veins, particularly when comparing wings of fairly distant groups. The above conclusion was first of all reached on the ground of the evidence that in a series of cases morphologically similar veins are seen to be differently disposed in the wings of the representatives of certain groups, a fact depending apparently upon the demands of mechanics. This may be exemplified by the distribution of veins noted by Martynov (1938) in the members of the family Euthygrammidae, where mediana anterior (MA) is a concave vein, and mediana posterior (MP) a convex one (a location directly opposite to that established for those veins by the terminology based on Lameere's theory). As to CuA and CuP, both of them are found to be concave veins, whereas on the theory just referred to CuA ought to be a convex vein (see fig. 1). Moreover, Martynov points out that in the families Tettigoniidae and Haglidae, as well as in Gryllidae males, CuA is a concave vein while CuP is a convex one, a condition which totally disagrees with the rule of Lameere, differing at the same time from what may be seen in that respect in the representatives of the family Euthygrammidae. Both the latter and the above-mentioned families belong to Orthopteroids, in other words, all these groups are united together by a

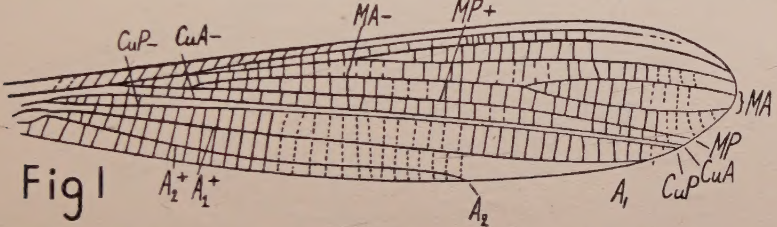

Fig. 1.—*Euthygramma parallellum* Mart. Fore-wing. After Martynov.

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common root of origin, although they may differ from each other. But, as the matter stands, there is practically no uniform scheme in the distribution of convex and concave veins, for they are quite variably arranged to meet the demands of the wing's mechanical structure. Thus, for example, in the genus *Euthygramma*, where CuA and CuP are very closely spaced, and in the living insect should have formed one common mechanical system playing a general part in the consolidation of the wing, these veins had inevitably to occupy an identical position. They are found, therefore, to lie in the hollow of the wing as concave veins.

Occasionally the same vein may be represented in various parts of the wing either by a concave or a convex vein, which fact may likewise be connected

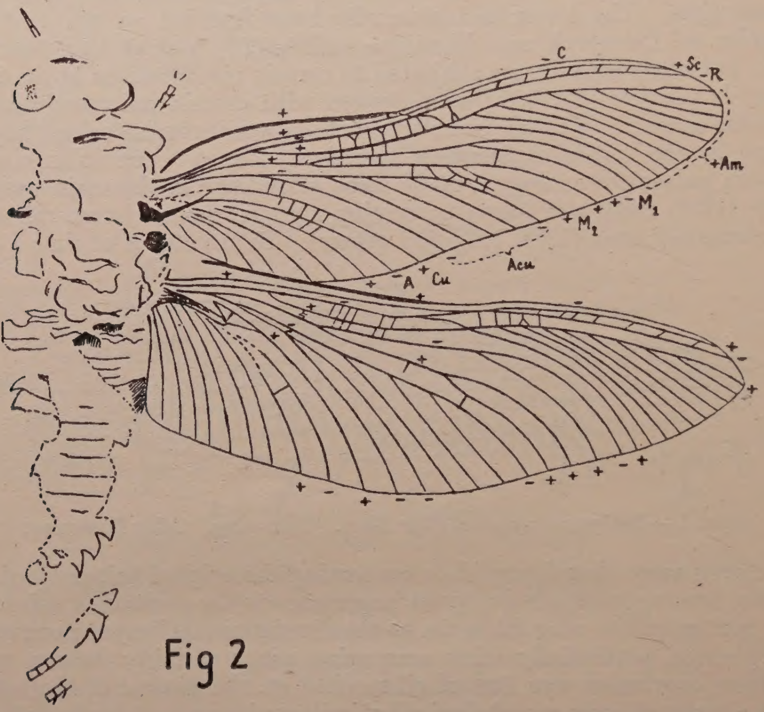

Fig. 2.—*Doropteron mirum* Zalessky. Notation according to the author.

with structural peculiarities. A similar condition occurs in dragon-fly wings, *e.g.* among the members of the genus *Aeshna* whose costal vein is convex as far as the nodulus, becoming concave beyond the latter. It is true that in this case a free concave Sc extends to the nodulus, disappearing farther on, and seeming to take part together with C in the formation of the costal margin.

In the fossil odonatoid insect *Doropteron mirum* G. Zalessky recently discovered by me and separated into a new Order Hemiodonata, the abovementioned disposition is still more pronounced. In that form Sc is entirely divided from C all over its length, as well as beyond the formation homologous with the dragon-fly subnodulus. Nevertheless, in this case, too, C runs as a convex vein up to the mid-wing, changing into a concave one farther on (see fig. 2). These and similar facts, for which there is not adequate space for a full discussion here, serve to show the absence of any strict connection between the convex and concave position of veins in the wing and their homology. The distribution of veins is exclusively determined by the demands of mechanics and the requirements of the wing construction for the most efficient fulfilment of their function. When a definite alternation of convex and concave veins is once developed, and established within the range of a certain individual group, it becomes more or less constant. In many cases it is possible, therefore, to take into account the convex or concave situation of a wing vein and to utilise that character as a criterion in determining the given vein, and in homologising it with those of related and similar forms. Dr. J. Needham (1935), an authority in the matter of wing-venation and tracheation, has ultimately come to the same conclusion. My own ideas concerning the formation of venation and its principal rules are mostly in agreement with those of that author as stated in his paper of 1935. I think it impossible, however, to attribute too great a significance to the wing-tracheation as a base on which veins are laid down, the same opinion being already advanced by Martynov (1924). Needham (1935 : 113) believes the formation of veins to be first of all conditioned by the hypoderm and tracheae. In this connection the leading part played by the hypoderm ought to be emphasised, because there are veins with no tracheae at all, their absence indicating that, as a principle, veins may be formed without the participation of tracheae.

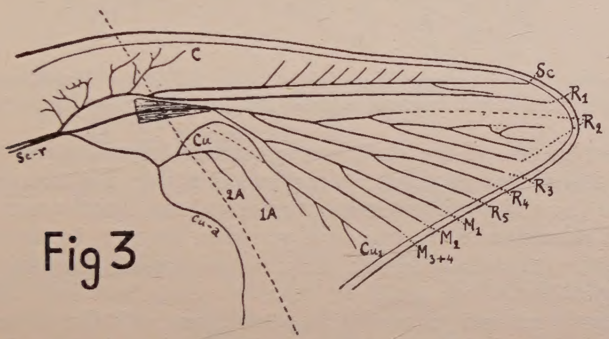

Fig. 3.—The fore-wing tracheation of the nymph of *Ameletus ornatus* Eaton. After Tillyard.

Between tracheation and venation a complete conformity is not always to be found (Needham, 1935 : 115; Comstock and Needham, 1898–1899), and in many holometabolous insects veins are formed before tracheae have penetrated therein (Needham, 1935 : 115; Marshall, 1913; Köhler, 1940). In mayflies tracheae and veins are in close correspondence with each other, although in this case, too, deviations may be seen to occur (Tillyard, 1923 : 156) (fig. 3). Sometimes tracheae are found to arise in a way dissimilar from the main tracheal trunk and to be variously correlated (Tillyard, 1923 : 155–156).

Although tracheation and venation are connected with one another, that connection, in some cases, is not deep enough to allow us to admit a greater importance to the relationship between tracheae and veins in elucidating the vein homology, than to the discrimination of convex and concave veins. In investigating the wing-venation of primitive and archaic Orders, where the correlation between tracheae and veins nearly coincides, ontogenetic data prove to be still of a certain significance. For more specialised and perfect

Orders the above fact is of much less importance, even of none, in certain instances.

In my opinion it would be reasonable to consider the hypoderm as playing a predominant rôle in the formation of venation. As to tracheae, they only serve as a frame to which venation is occasionally adjusted. In other cases as, for example, in holometabolous insects, it is the tracheae that adapt themselves to a freely developing venation. The connection between tracheae and venation is determined by a combination of two necessities, viz. the most rational concentration of the chitinous substance consolidating the wing, and a conjoined utilisation of those strengthened points for the distribution of tracheae. In the origin, phylogenetic formation, and development of the wing, everything is subordinated to one chief purpose, namely, to the most effective realisation of the function of flight; the main causes conditioning the processes named being those which serve to improve that function. The evolution of the wing structure has proceeded in accordance with the demands of mechanics, which differ somewhat in the case of the fore-wing and elytron from those of the hind-wing, that difference having affected in varying degree the structure of fore- and hind-wings. The view that the formation of venation has proceeded in conjunction with requirements of a mechanical nature has been already suggested by some earlier investigators (*e.g.* by Martynov in 1924), and taken into account by many recent writers; my present aim is only to call attention to that fact again. If the development of venation is affected by the demands indicated above we should take them into consideration when homologising the veins.

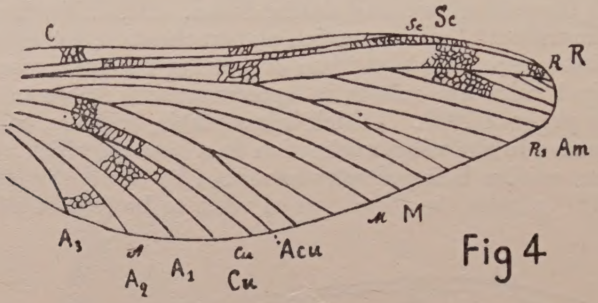

Fig. 4.—The wing of *Dictyoneura libelluloides* Goldenb. After Handlirsch. Venational notation after Handlirsch is given in italics, that of the author in roman letters.

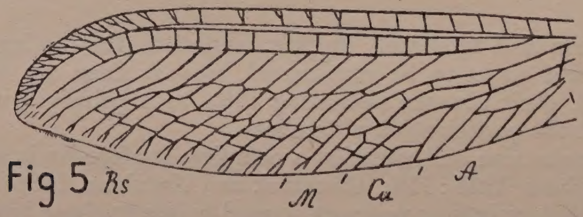

Fig. 5.—The wing of *Mesochrysopa zitteli* Meunier. After Handlirsch (× 2).

In the wings of ancient insects, Palaeodictyoptera, the vein usually termed the radial sector (RS) is very frequently a well-developed vein, forming together with its branches a fairly isolated mechanical system unconnected with R, *i.e.* a separate structural element.

The list given below contains examples of such a condition in Palaeo-

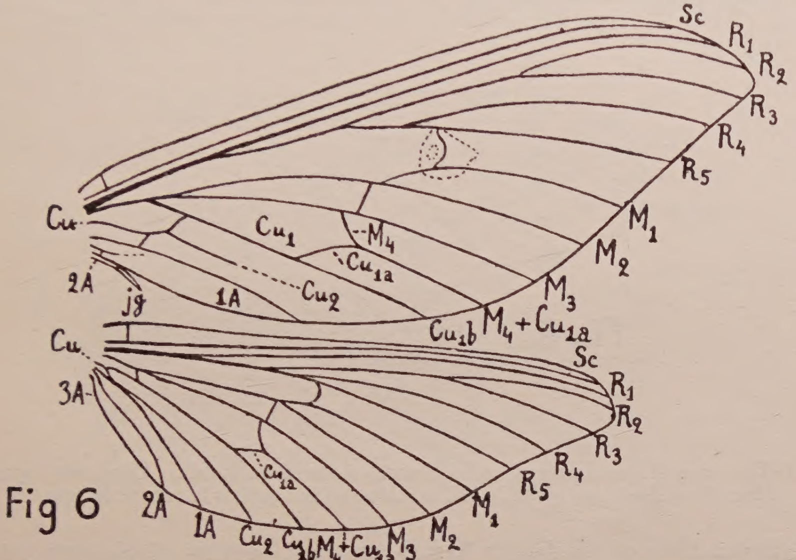

FIG. 6.—Venation of the fore- and hind-wing of *Leto staceyi* Scott. After Tillyard. Notation according to the same author (× 0·8).

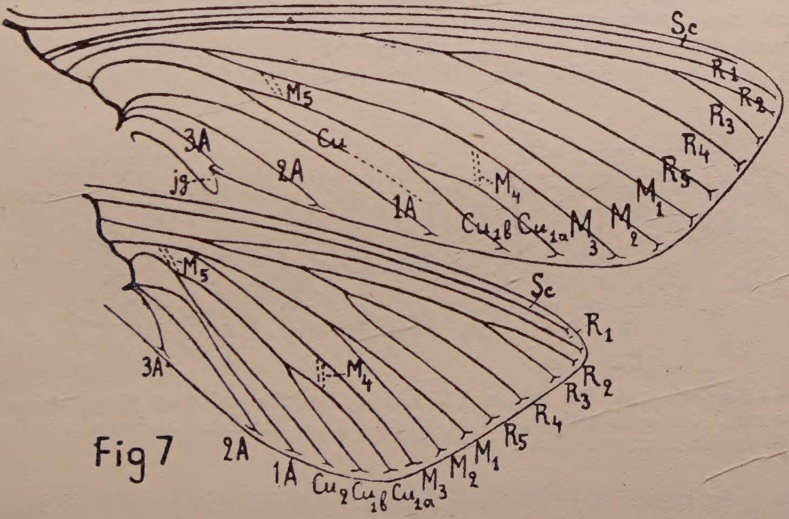

FIG. 7.—Wing-tracheation of a newly formed pupa of *Charagia splendens* Scott. After Tillyard (× 3·4).

dictyoptera, Protorthoptera and Protoblattoidea, together with references to the tables and figures reproduced by Handlirsch in his book *Die fossilen Insecten*, etc. of 1908. Some of those examples are shown in figs. 5, 6 and 7 of the present paper.

Examples from a number of representatives of the order Palaeodictyoptera:—*Haplophlebium barnesii* Scudder (Plate IX, fig. 9); *Dictyoneura libelluloides* Goldenb. (Plate IX, fig. 9) (reproduced as fig. 4 of the present paper); *Goldenbergia elongata* Goldenb. (Plate IX, fig. 18); *Acanthodictyon decheni* Goldenb. (Plate IX, figs. 20 and 21); *Eurythrompteryx antiqua* Handl. (Plate X, fig. 16).

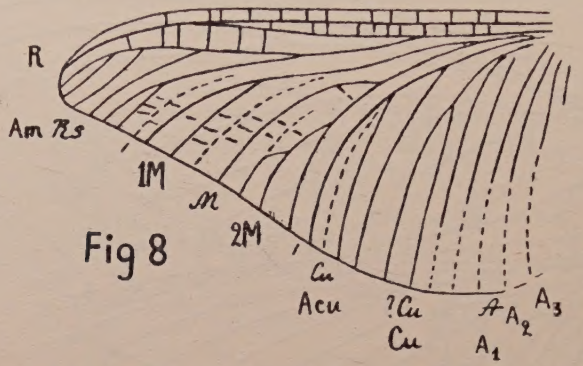

FIG. 8.—The wing of *Pseudoborrea boulei* Meun. After Handlirsch. Venational symbols after Handlirsch are given in italics, those of the author in roman letters.

Representatives of the family SPILAPTERIDAE:—genera, *Spilaptera, Bacuerelia, Compsoneura, Homaloneura, Homaloneurites*, etc. (Plates XI and XII), *Lamptroptilia grand'earyi* Brongniart, and *Lamproptila stirrupi* Brongniart (Plate XII, figs. 8 and 9), *Polycreagra elegans* Handl. (Plate XII, fig. 10). *Comptezoneura reticulata* Handl. (Plate XII, fig. 22) and others.

Turning to other Orders of fossil insects, we find rather numerous cases of RS being a structural element fairly independent of R, which feature occurs, for example, among the representatives of the Order Protorthoptera, namely in *Spaniodera ambulans* Handl. (Plate XIII, figs. 10, 11 and 12), *Propteticus infernus* Scudder (Plate XIII, fig. 14), *Dieconeura arcuata* Scudder (Plate XIII, figs. 20 and 21) while in *Belichia wettinensis* Schlechtendal (Plate XIV, fig. 23) RS arises quite freely from R even at the base of the wing.

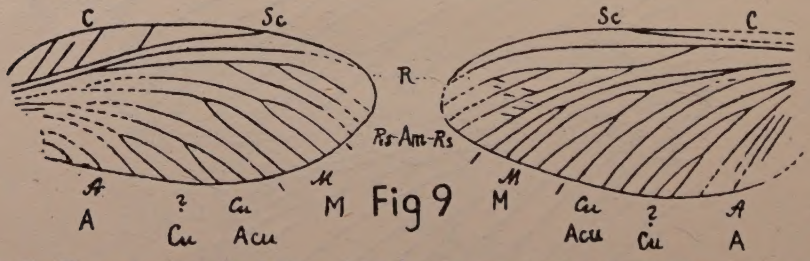

FIG. 9.—Fore-wing (on the left) and hind-wing (on the right) of *Mecynostoma dohrni* Brongn. After Handlirsch. Vein notation after Handlirsch is given in italics, after the author, in roman letters.

The same may be seen to take place among Protoblattoidea, *e.g.* in *Stenoneura fayoli* Brongniart (Plate XV, figs. 16, 17, 18), *Anthracothremma robusta* Scudder (Plate XVII, fig. 8).

Being unable to cite many examples in the present brief communication, I find it still pertinent to point out that in mayflies there may be found a well-marked separate position of a vein which has been labelled as RS by certain authors (Comstock, Needham, Martynov, Tillyard and others), and as M by Anna Morgan, though later, in 1918, Comstock adopted Morgan's interpretation. In many mayflies, particularly in fossil PROTEREISMIDAE, RS runs from the very base without coming into contact with R. In more specialised and perfect insects no connection is seen to exist between RS and R, *e.g.* in Neuroptera

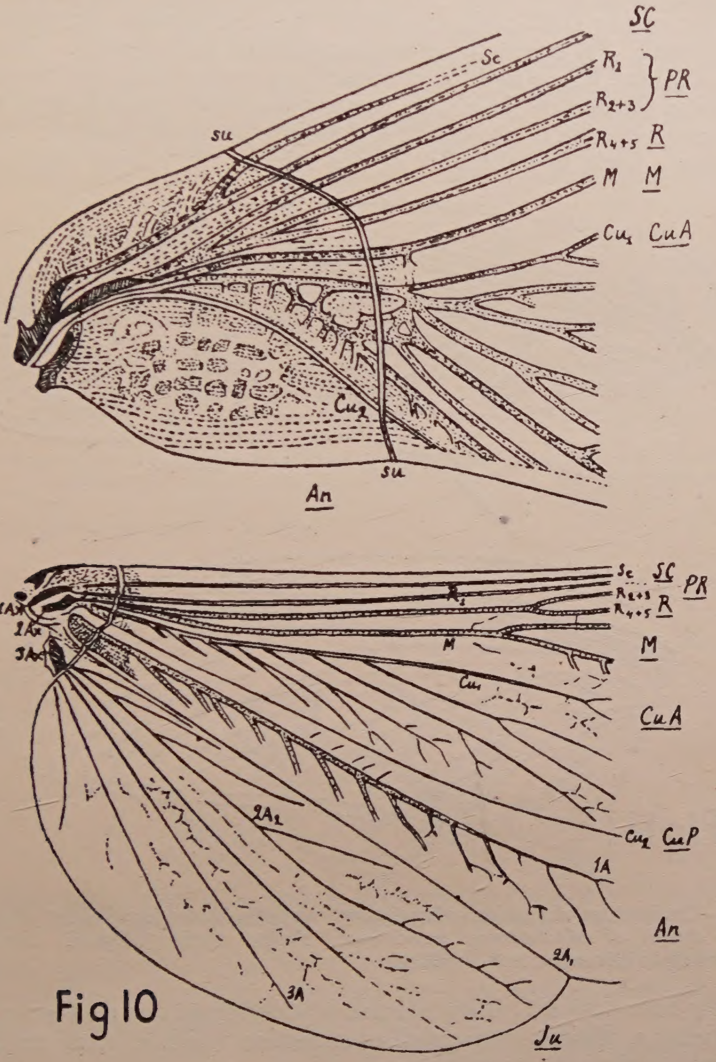

FIG. 10.—The main parts of the fore-wing (above) and the hind-wing (below) of *Mastotermes darwiniensis* Frogg. Imago. After Tillyard. Non-underlined venational notation after Tillyard, underlined one after Martynov. In-jugal region of the hind-wing.

(fig. 5) and in some butterflies (figs. 6 and 7) of the suborder Jugata (Tillyard, 1919 : 645 and 646).

In the wing of termites (figs. 10 and 11) in front of the radius (R) there lies a vein termed by Martynov (1937) the preradius (PR), a name which had already been given to the same vein of the cockroach hind-wing (1923). According to that author (1923 : 96), the radius of the cockroach corresponds to RS of other insects, PR being, therefore, homologous with their R. Those veins, *i.e.* R (= PR) and RS (= R of the cockroach) represent totally free morphological structures in the most archaic form *Mastotermes darwiniensis* Frogg., belonging in Martynov's opinion to an ancient and archaic group of termites. In Palaeodictyoptera a fairly free situation of two veins of the cubital region has very frequently been noticed. They become detached from one another very early, each forming a distinct mechanical construction which in some cases is even wholly isolated from the very base.

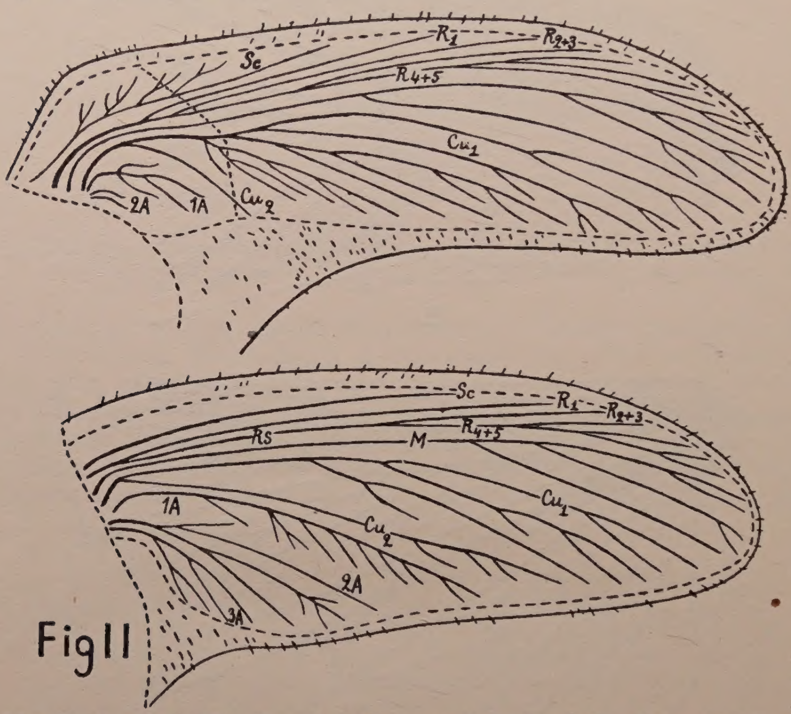

Fig11

Fig. 11.—Tracheation of the fore-wing (above) and the hind-wing (below) of the nymph (last stage) of *Mastotermes darwiniensis* Frogg. After Tillyard. Nomenclature according to Comstock and Needham.

Examples : *Dictyoneura libelluloides* Goldenb. (fig. 4), *Eurythrompteryx antiqua* Handl., *Spiloptilus ramondi* Handl. (Handlirsch, 1908, Plate XI, fig. 14). Suitable examples are also afforded by *Pseudoborea boulei* Meunier (fig. 8), *Anaxion boulei* Meun. and *Mecynostoma dohrni* Brongn. (Handlirsch, 1919, figs. 20, 21, 26 and 27).

In mayflies, too, Cu_1 and Cu_2 are isolated enough, forming wholly separate veins in some cases. In other more specialised insects Cu_1 and Cu_2, while arising from a common base, very often constitute distinct mechanical elements, their dissociation beginning as early as at the very base of the wing. In termites such as *Mastotermes* Cu_1 and Cu_2 run quite separately throughout their length, while tracheae in the wing rudiments of their nymphs very soon become isolated from each other.

Thus, R and RS are of old unconnected independent veins or structural elements. In a number of specialised types they are sometimes closely joined together and have a sufficiently long common base, whereas in others they retain a fairly conspicuous freedom. To that isolated vein, which is usually interpreted as a branch of R and called RS (Morgan termed it M in mayflies), I assign the name antemediana (Am), because that vein cannot be considered as a branch of R, being sometimes either entirely free or connected with M. But the radius R is often seen to possess branches, some of which attain a certain degree of isolation. Such a detached branch of R, usually represented by the same convex vein, as is also R, may be called RS. In order to avoid misunderstandings it would be preferable, however, to discard the symbol RS and to label the branches of R as R_1, R_2, R_3, and so forth.

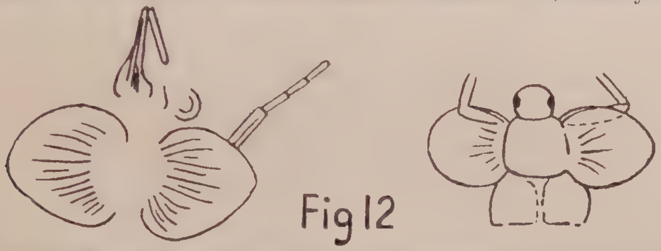

FIG. 12.—Wing appendages in the prothorax of representatives of the order Palaeodictyoptera. On the left *Lithomantis carbonaria* Woodw. (× 1). After Handlirsch (a detail of the figure). On the right *Stenodictya lobata* Brongn. (× 1). After Brongniart from Handlirsch (a detail of the figure).

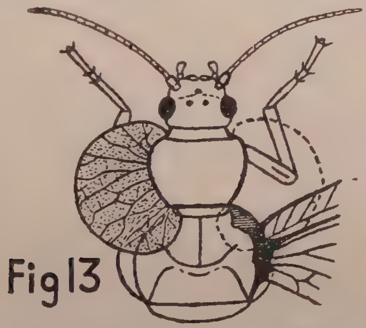

FIG. 13.—The anterior part of the body of *Lemmatophora typica* Sell. A representative of the Order Protoperlaria. A detail of Tillyard's restoration.

Instances of an isolated position of Cu_1 and Cu_2 in Plectoptera and Isoptera as well as an occasional occurrence of a complete disunion of veins of the cubital region in Palaeodictyoptera show that in the latter region there have always existed two separate morphological structures, two distinct mechanical constructions termed by me antecubitus (Acu) and cubitus (Cu). These terms Acu and Cu sometimes serve to designate the same veins which according to the notation of other writers are called either Cu_1 and Cu_2 or CuA and CuP. But in some cases my Acu corresponds to Cu of those authors and Cu to their first anal vein—A_1 (fig. 14).

The wing rudiments or primitive wings of the ancestors of Pterygota were probably like those (alulae) found on the prothorax of ancient extinct insects, such as Palaeodictyoptera and Protoperlaria (figs. 12 and 13). Even before becoming a more or less definite flying organ, the primitive wing had been a rounded lateral protuberance of the insect's body covered with main longitudinal veins quite freely distributed, diverging radially from the base of the wing, and provided with tracheae from two sources on the tracheal trunk of the body; one of them showing that relationships between tracheae and veins were developing in the process of wing evolution, while neither the former nor the latter had been predetermined by the other.

The wings of different insects afford us diverse examples of evolutionary stages, but, nevertheless, we may everywhere find the same chief mechanical primitive wing elements which in various combinations have produced the wing structure of the more perfect and specialised forms. The above elements involve those main longitudinal veins which, in the course of evolution of all insects from primitive, ancient and archaic types to perfect and specialised ones, have been to a lesser or greater extent simple veins, or isolated mechanical systems (except in the case of the most specialised forms). To such veins belong costa (C), subcosta (Sc), radius (R), antemediana (Am), mediana (M), antecubitus (Acu), cubitus (Cu) and the anal veins (A) varying in number. In front of the costal vein there is sometimes found one precostal vein P or even more than one, especially when the costal field is well developed.

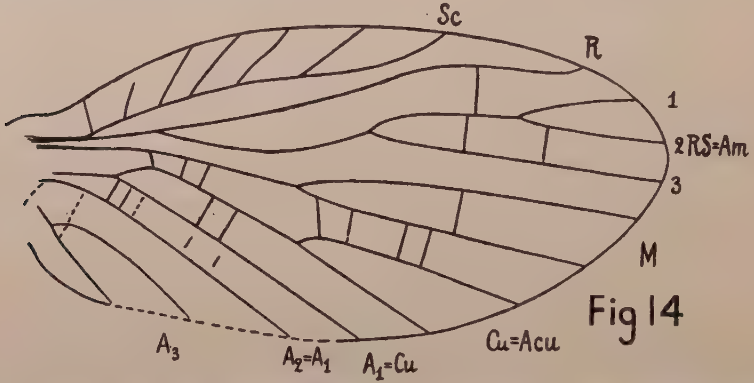

FIG. 14.—The fore-wing of *Permosialis paucinervis* Martynov. After Martynov with that author's notation. Corresponding terms from the present writer's nomenclature are given with the sign =.

Each of these main veins can give off a series of branches, some of which may attain a sufficient structural independence. This fact may be exemplified by M, which is very frequently represented by two main branches M_1 and M_2 or, as I prefer to call them, by 1M and 2M. This condition served as one of the causes for dividing them into MA and MP, but unlike R and Am as well as Acu and Cu, these two branches are never completely free even in archaic primitive forms. On the contrary, this particular vein is often seen to form a single mechanical construction, as, for example, in termites.

The present paper is concerned neither with the problems of a practical application of a new venational nomenclature nor with those of homologising venation in connection with its use, but in a brief statement of certain reasons which have induced me to change the former nomenclature, and to establish new conceptions and the terms " antemediana " and " antecubitus ",

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A NOTE ON *PHANUROPSIS SEMIFLAVIVENTRIS* GIRAULT (HYM., SCELIONIDAE), AN EGG-PARASITE OF CACAO STINK-BUGS

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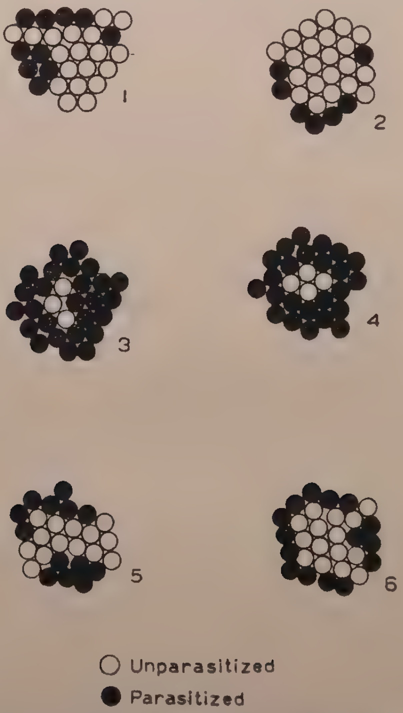
Various species of stink-bugs have been recorded (Callan, 1944) as feeding on cacao (*Theobroma cacao* L.) in Trinidad, B.W.I. The commonest species are *Mecistorhinus picea* (P.B.) and *M. tripterus* (F.), which are sometimes sufficiently abundant in cacao nurseries and propagators to rank as minor pests.



Figs. 1–6.—Egg-masses of *Mecistorhinus tripterus* (F.) showing extent of parasitism by the Scelionid egg-parasite, *Phanuropsis semiflaviventris* Gir.

All the species of *Mecistorhinus* appear to have very similar habits. The eggs are laid in a compact mass attached to the underside of a cacao leaf. Each egg-mass usually contains from 25 to 30 eggs. Parental care is exhibited by the female brooding solicitously over the eggs and subsequently remaining for a time in close proximity to the newly hatched nymphs. This habit has been supposed to confer some protection against egg-parasites and predators

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of both the eggs and young nymphs. The presence of the brooding female probably deters predators from attacking the eggs and young nymphs, but the eggs are often highly parasitised.

Phanuropsis semiflaviventris was described by Girault (1916) as a new genus and species of Scelionid reared from hemipterous eggs from Trinidad. I have reared this species on numerous occasions as a very common egg-parasite of the cacao stink-bugs, *Mecistorhinus picea* and *M. tripterus*, in Trinidad.

Unparasitised egg-masses of these stink-bugs were only very rarely found. Most egg-masses showed a rate of parasitism of from 25 to 90 per cent. In the six egg-masses diagrammatised in figs. 1–6 there are a total of 169 eggs, of which 95 are parasitised and 74 unparasitised, giving an average rate of parasitism of 56 per cent. No egg-masses were found in which every egg was parasitised.

It is apparent from figs. 1–6 that the eggs towards the exterior of the egg-mass are almost always parasitised and those in the centre are unparasitised. This is naturally more evident in figs. 3–4, in which parasitism is high, than in figs. 1–2, in which the egg-masses are less highly parasitised.

This observation, together with the fact that no egg-masses have been found completely parasitised, indicates that the presence of the brooding female is responsible for the partial protection of the egg-mass from parasitism, the eggs in the centre remaining unparasitised while the peripheral eggs are almost invariably attacked by the parasite.

ACKNOWLEDGEMENT.

I am greatly indebted to Dr. C. F. W. Muesebeck, United States Department of Agriculture, Washington, D.C., who kindly determined specimens of *Phanuropsis semiflaviventris* Gir.

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HOMOEOSIS IN *PSYCHODA PHALAENOIDES* L. (DIPTERA)

By E. A. COCKAYNE, M.A., D.M., F.R.C.P., F.R.E.S.

THE abnormal male of *Psychoda phalaenoides* L. was taken at Appleby, Westmorland, in September 1942, and I am indebted to Dr. Llewellyn Lloyd for sending it to me. In the male of this species there are a pair of dorsal outgrowths, the cercopods, each clothed with simple setae and with a large flattened seta, the retinaculum (tenaculum of Feuerborn), directed inwards arising from a socket of thickened chitin at the tip. There are also a pair of ventral outgrowths, gonopods, consisting of two segments, a proximal one, the coxite, and a distal one, the style. The coxite has a large oval area on its outer aspect covered with long setae arising from special sockets, and the style has simple short setae arising from circular flat sockets. Between the ventral appendages lies the aedeagus, a straight tubular organ with an eversible lining covered with small recurved spines. On emergence the tip of the abdomen of the male rotates through an angle of 180°, so that the dorsal parts appear to be ventral and the ventral parts dorsal.

In the abnormal specimen the dorsal outgrowths, the cercopods, and the left ventral outgrowth, are normal, but the right ventral outgrowth has no clear division into two segments. The coxite is aborted and is only recognisable by having a very small oval area on its outer aspect covered with special hair sockets. The style is very large, too long and too broad, and is irregular in outline. At a point on the internal aspect towards the distal end there are four large sockets with thickened chitin round their rims, and from each of them arises a large flattened seta identical in structure with the retinaculum of a cercopod.

According to Tonnoir and Edwards, the appendages with two segments, coxite and style, are borne on the ninth sternite, so that the style is equivalent to the stylus of the lower insects, and is homologous with a leg, while the cercopods arise from the outer corners of a quadrate plate, which is the tergite of the ninth somite. If these authors are correct, the cercopods are accessory outgrowths without homology outside the lower Diptera.

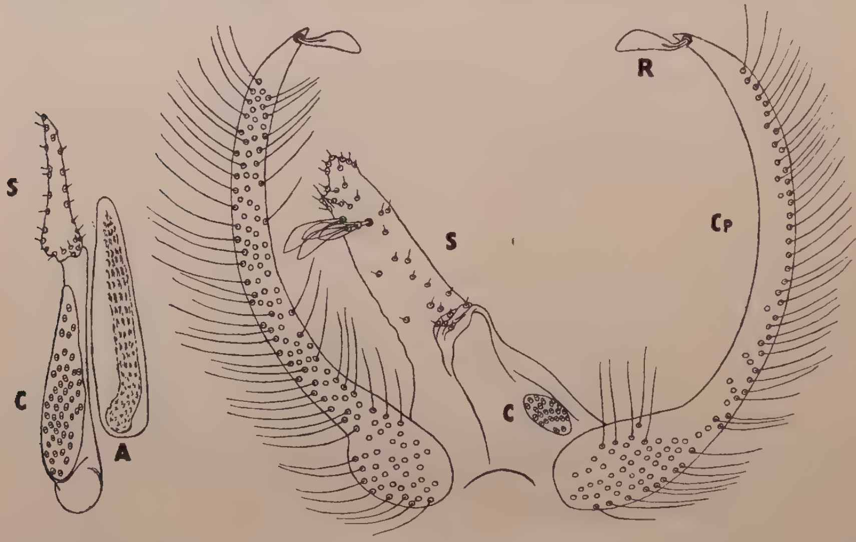

FIG. 1.—Cp. = Cercopod. R = Retinaculum. C = Coxite. S = Style. A = Aedeagus. The left style and the aedeagus were separated from the rest of the hypopygium in the routine method of preparation.

On the other hand, Feuerborn, though he agrees that the coxite and style arise from the sternite of the ninth somite, says that the quadrate plate from which the cercopods spring is the tergite of the tenth somite and that it has a spiracle and the anus situated between the bases of the cercopods. He regards the cerçopods as cerci homologous with legs. Dr. Lloyd, who has given me this information, says he has seen the anus and spiracle clearly in *Psychoda alternata* Say, but not in other species which he has examined. Thus according to Feuerborn the coxites and styles are the true appendages of the ninth somite and the cercopods those of the tenth, both being homologous with a pair of legs. The abnormal specimen fits in better with Feuerborn's view than with that of Tonnoir and Edwards. For it is much more likely that an appendage of one somite should show some or all of the structural characters of an appendage of another somite and thus fulfil Bateson's definition of homoeosis, than that an appendage should show some of the structural characters of an accessory outgrowth in no way homologous with it. There are numerous examples of homoeosis known in insects, in which an appendage of one somite resembles in structure that of another, but I know of no example of an appendage with the structure of an outgrowth not homologous with it or vice versa. Some apparent exceptions are given in my paper published in 1926, such as a *Parasemia plantaginis* L. with miniature wings replacing the hind legs. These, however, are not exceptions, if, as some think, wings are homologous with legs. It is more probable that this specimen and others like it are double monsters and not examples of homoeosis, but it is improbable that the abnormal *Psychoda* is a double monster, because the altered gonopod arises in the normal situation. I am therefore inclined to accept Feuerborn's view in preference to that of Tonnoir and Edwards, and to regard the specimen as an example of homoeosis as originally defined by Bateson.

If, however, it were an example of simple homoeosis, the abnormal coxite and style should be no larger than normal ones and there should be only one retinaculum. It is possible that it is an example of homoeotic reduplication due to injury at an early stage of development. There is no indication of division of the abnormal style into a triple organ, but it may nevertheless be a triple organ with the three parts fused, as is not uncommon in insects. The retinacula are merely specialised setae and, since they are not appendages, Bateson's law would not apply to them, and they would not be expected to be triple or to stand in mirror-image relationship with one another. Judging by their position, all four belong to the original style or, less probably, to one of the extra styles, if the supposition that homoeotic reduplication has occurred is correct.

It is interesting that in *Psychoda* (*Philosepedon*) *humeralis* Meigen there are two retinacula on each cercopod, and that in some other genera of PSYCHODIDAE such as *Trichopsychoda*, *Pericoma*, and *Telmatoscopus*, there is a bunch of retinacula, up to four or five in number, on each cercopod. This makes it necessary to consider whether the abnormal *P. phalaenoides* shows a reversion to an ancestral condition, but there is little to commend this hypothesis, for it is the abnormal style and not a cercopod that bears the four retinacula. It would therefore be an example of homoeosis with reversion to an ancestral condition. This explanation is more complicated and for this reason alone more improbable than that of homoeotic reduplication.

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THE COPULATION AND THE TERMINAL SEGMENTS OF DIPTERA

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I. Postures of Flies Found Coupled Together.

Some authors have given accounts of the coupling of flies and have noted vagaries in these habits. C. G. Lamb (1922, *Proc. Roy. Soc.* (B) **94** : 1–11) used the Diptera in his account of " The geometry of insect pairing." H. J. Feuerborn (1922, *Zool. Anz.* **55** : 189) discussed " Das Hypopygium inversum und circumversum." O. W. Richards (1927, *Biol. Rev.* **2** : 322–8) discussed " The mechanical relations of the male and female genitalia " when reviewing " Sexual selection and allied problems in the insects." G. H. Hardy (1935, *Ann. Mag. nat. Hist.* (10) **16** : 419–434) summarised his observations in " The positions assumed by copulating Diptera."

No other Order of insects exhibits such a wide variety of these habits or so needs special consideration and standard terms for recording them. The manner in which authors have expressed their observations has led to apparently contradictory statements, and this is producing some confusion. To the few satisfactory terms hitherto proposed others are added here to cover all body positions yet known and also the general features associated with these postures. The details of the interlocking mechanism need investigation anew, and only the correlation between the aedeagus and vagina (discussed below) is yet assured.

The present discussion leads to an understanding of the homologies of sclerites of the terminalia of the Orthorrhapha and Cyclorrhapha, about which there have been many views expressed, none proving satisfactory. The solution to this problem arises from a study of Feuerborn's hypopygium circumversum and the complex way in which this has been brought about.

Terminalia. This term is used throughout this paper to cover those terminal segments of the abdomen, of both sexes, that are modified or incorporated in the genital apparatus. It is the postabdomen of some authors, the anterior set of segments being the preabdomen. The term *hypopygium* applies only to the ninth and tenth segments and appendages of the male.

Rectilinear male terminalia. The abdomen in most males forms a straight line, so that all segments are in a linear series which Lamb refers to as symmetrical. Normally the aedeagus is directed posteriorly and only in the case of the " circumverted terminalia " is it permanently directed anteriorly.

Curvilinear male terminalia. The male may have the terminal segments strongly bent so as to lie in a series along a curved median line and they are then referred to by Lamb as being asymmetrical. Lamb's term is liable to confuse the understanding of this condition as authors usually refer to asymmetry, especially of the aedeagus, in forms to which Lamb ascribes a symmetrical hypopygium. The curvilinear condition is found in Empididae, Dolichopodidae and Syrphoidea, and it stands between the normal and the circumverted terminalia, both belonging to the rectilinear condition. The aedeagus is directed dorsally, ventrally, laterally or anteriorly and never posteriorly in the various curvilinear forms.

Body-line. When the sexes are pairing, the median longitudinal axis of the couple varies in direction. The line from head to head may be expressed as U-shaped, V-shaped, angular, straight, and in other ways. The position taken at the instant of coupling, called the " pose " by Lamb, may change at a later period to another posture to which Lamb restricts the term " position," but the last is inconvenient for adoption here.

Horizontal poise. Most flies copulate with their bodies held more or less parallel to the ground and most of the figures in the diagram illustrate this poise. The male, however, may take some other position.

Vertical poise (fig. 12). Certain flies that hover in the air may couple and remain with their bodies more or less vertical, their heads being uppermost, forming a more or less U- or V-shaped body-line.

Terminalia erect. When the male has its terminalia definitely fixed in the one position, with the anal papilla lying above the rearwardly directed aedeagus, the terminalia are regarded as being in the erect position. This is the " hypopygium normal " of Richards.

Terminalia diverted. Many flies have the male terminalia set rather loosely along the longitudinal axis, so that the parts are found in any position from the erect to the rotation of 180 degrees. When coupled they take the complete turn of the half-circle.

Terminalia inverted. Sometimes the terminalia of the male are more or less fixed in the inverted position, the aedeagus lies above the anal papilla, being turned through 180 degrees. This is the " hypopygium inversum " of Feuerborn.

Terminalia circumverted. Feuerborn thought that in Muscoidea the hypopygium was rotated through a full circle of 360 degrees. The evidence lies in the fact that in this sex the apical section of the genital passage takes a loop completely round the alimentary canal. Little evidence could be gained by the examination of external parts, including tergites and sternites, and he described this condition by the term " hypopygium circumversum."

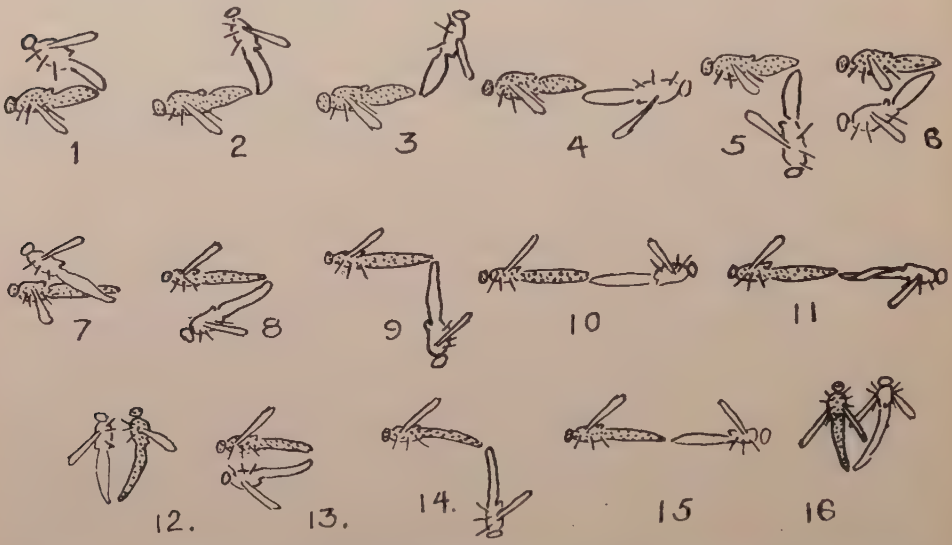
Lamb drew attention to Lowne's statement that the male *Calliphora* has the sclerite of the eighth segment quite asymmetrical, whilst Keuchenius found that the testes were nearly always placed asymmetrically; from this Lamb seems to deduce that the terminalia of Muscoidea could become modified from the Syrphid type with which he dealt, and in the present paper this solution is found correct.

Richards referred to papers by Minchin and Tulloch which anticipate Feuerborn's discovery of the loop, but Feuerborn is the only author who attempted to explain it. It has been suggested that the same condition occurs in Syrphoidea and perhaps EMPIDIDAE and DOLICHOPODIDAE, but it seems very doubtful if this is so in the two latter, the suggestion arising from a misunderstanding of the facts.

The phylogenetic development of the circumverted terminalia apparently is that of having passed from the erect to the diverted and to the inverted terminalia. When in the last state, the curvilinear development of the terminalia transferred the inverted posteriorly directed aedeagus to an anteriorly directed one. Later the anus moved from a plane lying below the aedeagus to one lying above it. In this manner the spiral encirclement of the alimentary canal was completed. The segments of the curvilinear terminalia reformed themselves back to the rectilinear type during the process.

The circumverted hypopygium is only a modified form of the inverted hypopygium, and the idea that the hypopygium had turned through 360 degrees, which idea seemed so incredible to, yet was accepted by, Richards, may now be regarded as a misunderstanding. Authors had overlooked the fact that the aedeagus had remained inverted in an apparently erect hypopygium.

Direct interlock. When the male and female terminalia couple together, it is possible for the anal papillae, one on each sex, to remain adjacent to each other and lie in the one horizontal plane above the aedeagus. This condition is quite unknown in Diptera and is referred to as the direct correlation by Lamb. For the theory of the correlation, see part II of this paper.



FIGS. 1–6.—Positions assumed by copulating flies and the normal sequence of changes from the superimposed position (fig. 1) with the male above, to that with the female above (fig. 6).
FIGS. 7–11.—Another form of the superimposed position (fig. 7) and its sequence of changes to the opposed position (fig. 11) with the male abdomen twisted.
FIG. 12.—The vertical poise often adopted by mosquitoes.
FIGS. 13–15.—The normal form of the facing position (fig. 13) and its changes to the opposed position (fig. 15).
FIG. 16.—The pleural position, seen dorsally.

The dark fly represents the female and the white one the male. Nearly all the positions may become stable and those that have been given names are as follows. Superimposed, figs. 1, 6 and 7; opposed, figs. 4, 10, 11 and 15; pendant, figs. 5, 9 and 14; facing, figs. 12 and 13; pleural, fig. 16.

Diverted interlock. It may be possible for some insects to couple with their terminalia more or less askew, one to the other, the appendages of the male being asymmetrical so as to accommodate this arrangement. In this case the anal papillae may lie in different planes. Although asymmetry is found sometimes in the Diptera, it is not considered that this ever brings about the diverted interlock within the order.

Inverted interlock. In all cases known and suspected, the form of interlock is that with the male anus lying in the same vertical plane but on the opposite side of the aedeagus to that of the female anus. This is equivalent to the "inverse correlation" of Lamb, but the terms are not synonymous, as "correlation" applies only to the genital conduit, not to the interlocking.

Superimposed position (figs. 1, 6 and 7). One sex may lie immediately above the other, both facing the same way, during any part of, or the whole of, the copulation period. Either sex, but usually the male, lies above. When coupling is initiated in this manner, Lamb calls it the " vertical pose," which is not to be confused with the " vertical poise " defined above. Lamb refers to the male vertical pose and the female vertical pose in accordance with which sex lies above. When, however, the male passes the tip of the abdomen below, coupling in this manner (fig. 7), Richards calls it the " false male vertical pose."

Opposed position (figs. 4, 10, 11 and 15). Some flies are found with a straight body-line, facing opposite ways, the heads being at the maximum distance apart. When taking this attitude at the instant of coupling, Lamb calls it the " linear pose," and, if assumed later, the " linear position."

Diverted position. Occasionally a pair may be found in an abnormal position, a variant not usually met, sometimes having no stability and at other times becoming quite stable. The present term covers such cases. An example is seen in the genus *Neoaratus* (Asilini) which may revert towards the opposed position, but with the terminalia of both sexes angulated, one to the other, as there is no provision for the terminalia of either to accommodate the coupling in the undistorted opposed position.

This, apparently, is the primitive condition that leads towards the opposed position from the superimposed one. The next stage in the development is that accompanying the diverted terminalia of the male, where the hypopygium is able to be twisted at its base by rotating on its longitudinal axis. More rarely, as in *Trichoitamus* (Asilini), the female terminalia ovipositor, which consist of the eighth segment and proctiger, can be inverted, leaving the hypopygium in the erect position. The ovipositor is rubber-like and crumples up within the genital cavity of the male, the body-line changes from the superimposed to the opposed position, where it shows no deflection of the median line drawn from head to head, and the hypopygium retains the erect position. The final stage is reached with the inverted hypopygium upon which new developments lead to the circumverted terminalia.

Pleural position (fig. 16). Flies have been observed coupled side by side, their body-line more or less U-shaped. This feature is known to me only in MANTISPIDAE, a family of the Neuroptera which initiates coupling this way, and then takes up the opposed position. Richards calls this the " false linear pose."

It is not clear in literature if flies couple together in this way, but if so the method might be accommodated through the male passing the tip of its abdomen below that of the female, otherwise it seems essential that the male hypopygium must be inverted. If inverted, this may be regarded as a variation of the opposed or the facing position.

Facing position (figs. 12 and 13). The bodies of the couple may lie adjacent to each other, clinging by the legs, venter to venter, in what Richards calls the " belly to belly position," which is normally seen in CULICIDAE.

Pendant position (figs. 5, 9 and 14). One sex may lie in the horizontal position, and the other may hang down below, assuming a pendant position either with the legs facing towards the direction of flight or in the reverse direction. The hypopygium is erect in the latter case and inverted in the former.

Figs. 1–16 illustrate these varied positions in a manner that shows the usual method of passing from one coupled position to another.

Figs. 1 to 6 show the superimposed position (fig. 1) with the male uppermost, passing (figs. 2 and 3) to the opposed position (fig. 4) with the legs of the male directed upwards, to the pendant position (fig. 5) where the legs are directed away from the direction of flight, and ultimately to the superimposed position with the female above (fig. 6), and the male with its legs directed downwards.

Figs. 7 to 11 show the superimposed position (fig. 7) with the male terminalia coupling from below, from which the falling male (fig. 8) reaches the pendant position (fig. 9) with the legs directed away from the direction of flight. The male may swing farther and take the opposed position (fig. 10) with the legs directed upwards, but turns over to the upright position (fig. 11) with legs directed downwards. In this action the male abdomen takes the whole spiral, or the female may also aid by twisting its abdomen too. If neither sex may accommodate in this way, then the abdomens become angulated, one to the other, at least in respect to the terminal segments. If the male has the diverted terminalia then the body-line passes directly to that of fig. 15 instead of fig. 11.

Figs. 12 to 15 show the vertical poise (fig. 12) which may initiate coupling and in this pose only the facing position has been noted. Normally flies are found as seen in fig. 13. Here one sex only may lie in the horizontal plane, the other being at an angle making a body-line of V-shape up to 45 degrees. Apparently the female always lies above (fig. 13), from which the male may drop to the pendant position (fig. 14), the legs being towards direction of flight, but may pass to the opposed position (fig. 15) with the legs directed downwards.

Fig. 16 shows the dorsal aspect of the pleural position which has been recorded for Diptera.

The coupling together in the first instant usually is that of figs. 1, 7, 12, 13 and 15, the last not often being observed and that of fig. 16 has been recorded.

Stable positions maintained after coupling are represented by figs. 1, 2, 3, 5, 6, 7, 9, 11, 12, 13, 14 and 15.

Unstable positions are those of figs. 3, 10 and probably 16, but any of these may be held for a short time.

Although the postures given by figs. 5 and 9 are identical, they are reached through different forms of initial coupling, as also are those of figs. 4 and 10. Fig. 8 is inserted to illustrate the direction of the transfer from 7 to 9.

There is a noticeable trend towards varying the number of ways in which Diptera copulate, running parallel with the phylogenetic development of families, and reflected in the following divisions:—

Nematocera are found coupling together in positions illustrated in figs. 1, 12, 13, 15 and 16, and in addition may assume postures of varied kinds. Tabanoidea couple as in fig. 1, and assume postures 4, 5 and 15.

Asiloidea couple in positions 7 and often 1, whilst 6 has been recorded, and they subsequently adopt those of 6, 9, 11, 14 and 15, this variation being largely due to the appearance of the curvilinear male terminalia.

Syrphoidea couple as in fig. 1 and are seen in those of 6, 13 and 15 with certainty. Muscoidea couple as in fig. 1, and possibly also 2 if the male be extra small, and they may assume only those of 2 and 3, and possibly 4 as an accidental and unstable position. Here the curvilinear development disappears, leaving the terminalia always of the one form, the genital cavity opening on the ventral side, and the aedeagus inverted, all of which marks the typical form of the circumverted terminalia.

All flies with curvilinear terminalia, and those with rectilinear terminalia of the erect, diverted and circumverted form, initiate coupling in the superimposed position. Those flies with rectilinear terminalia and inverted hypopygium start in the facing or opposed position.

Table analysing the type of terminalia and the postures.

Posture of couple : fig.	Type of terminalia				
	Rectilinear				Curvilinear
	erect	diverted	inverted	circumverted	
1	×	×	—	×	×
2	—	—	—	×	—
3	—	—	—	×	—
4	×	—	—	?×	—
5	×	—	—	—	—
6	×	?×	—	—	×
7	×	—	—	—	—
9	×	—	—	—	—
10	×	—	—	—	—
11	×	—	—	—	—
12	—	—	×	—	—
13	—	—	×	—	×
14	—	—	×	—	—
15	—	×	×	—	×
16	×	—	×	—	—

II. THE THEORY OF CORRELATION IN THE PAIRING OF DIPTERA.

The theory of correlation, discussed by Lamb, is dependent upon the view that habits of copulation in Diptera are subservient to the need for keeping a direct correlation between the two essential parts of the terminalia, the aedeagus and the vagina. Richards, on the contrary, believed that throughout the order the aedeagus stands in inverse correlation with the vagina, and that all known facts agree with this assumption. On this account the whole thesis of correlation, as set down by Lamb, needs a fresh examination and amendment. The terms may be defined as follows :—

i. *Hypopygium.* The combined ninth and tenth segments of the male abdomen, fused together, and making a single unit which incorporates the aedeagus and the anus.

ii. *Hypopygium erect.* The anus lies in a plane above that of the aedeagus, and the ninth tergite lies adjacent to the eighth tergite.

iii. *Hypopygium inverted.* The anus usually lies in a plane below that of the aedeagus, but always the ninth tergite lies adjacent to the eighth sternite.

iv. *Aedeagus erect.* The true dorsum of the aedeagus lies in a plane nearer that of the anus than does its venter.

v. *Aedeagus inverted.* The true venter of the aedeagus lies in a plane nearer that of the anus than does its dorsum.

vi. *Genital conduit.* The conjunction of two separate tubes, the male genital tube and the female genital tube, to form a single tube in coition.

vii. *Genital correlation.* The mutual relationship of the dorsum and venter between the aedeagus and vagina.

viii. *Direct correlation.* The dorsum of the aedeagus is contiguous with the dorsum of the vagina when the genital conduit is formed.

ix. *Inverse correlation.* The dorsum of the aedeagus is contiguous with the venter of the vagina when the genital conduit is formed.

x. *Pose.* The position of the body of the male, relative to that of the female, at the instant when genital conduit is being established.

xi. *Vertical pose.* The sexes coupling together, one lying above the other, the heads facing the same way.

xii. *Linear pose.* The sexes coupling together with their bodies forming a line, the heads facing opposite ways.

The original intention, in using " vertical " and " linear " pose, was to make these terms also serve any variation derived from those two positions, but it has since been found that, in the theoretical sense, the two terms are nearly homologous. In Diptera the pose depends upon whether the hypopygium be inverted or erect. The inverted hypopygium, in its simplest form, is invariably associated with the linear pose in the accepted sense of Lamb, and of Richards, but the erect hypopygium combines the two.

Richards refers to the case where the male, lying above the female, passes the abdomen down to couple from beneath; he calls this the " false vertical pose " and the only difference lies in the female anal papilla being " free " and not in or near contact with the male abdomen.

The terms in *iv* and *v* do not belong to Lamb's paper, but are inserted here to mark the difference brought about in the terminalia of Muscoidea. Lamb not only overlooked the possibility of an inverted aedeagus, but also based the whole of his thesis on the assumption that he was dealing with an erect hypopygium in the curvilinear terminalia of *Eristalis*, which he studied.

Richards remarks on the circumverted hypopygium, " so that the relative positions of the anus and genital orifice are again apparently normal," overlooking the inverted aedeagus; nevertheless he correctly couples Muscoidea and Syrphoidea in the " hypopygium circumversum " without seeing that they were derived from the same curvilinear development of the terminalia.

Direct and inverse correlation are compared in figs. 17 and 18. The former illustrates the simplified coition when the sexes are collinear; the aedeagus and vagina come together as if in the direct correlation. Here the anus of one sex meets the other, which condition is never found in Diptera. This is the sense to which Lamb gives the term " direct " and it will be noted that the dorsum of the aedeagus meets the dorsum of the vagina, both marked by a thickened line.

Fig. 18 similarly illustrates the linear pose, the aedeagus and vagina meeting in the inverse correlation in the sense that Lamb gives the term " inverse." The hypopygium is inverted and the anus of the male lies below the aedeagus, so that it is remote from the female anus; it is the form invariably found in Diptera quite irrespective of the body-line adopted. It is noted that the dorsum of the aedeagus meets the venter of the vagina.

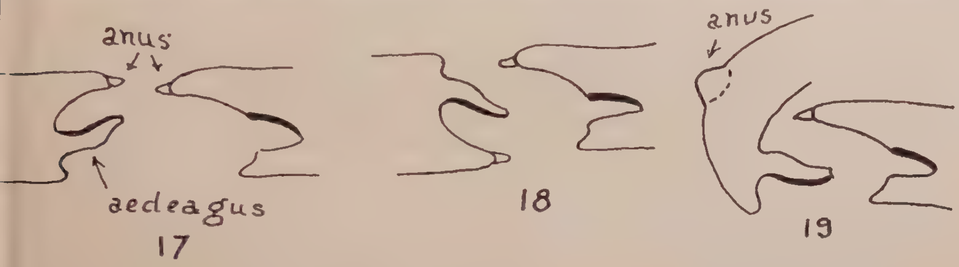
Fig. 19 illustrates the condition of inverse correlation found in Muscoidea, where the anus lies in a plane above that of the inverted aedeagus but still remains remote from the female anus. The pose here is vertical, the male lying above the female, but if the male were to be swung rearwards in the vertical plane, so that the sexes are collinear, then it becomes evident that the aedeagus lies above the male anus, which position is that of fig. 18.

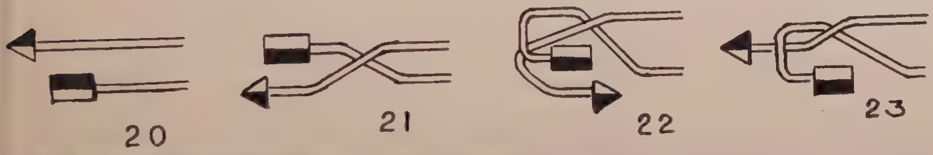
The inverted hypopygium is developed through a sequence illustrated by figs. 20 to 23, and this development explains how the passing of the genital duct over the alimentary canal can come about. Fig. 20 represents the relative position of the anus and aedeagus found in the erect hypopygium, directed rearwards, with their respective digestive and genital tracts. The anus, represented by a triangle, lies above the aedeagus, which is represented by a rectangular figure. The upper half of each is represented by a thickened line in all four figs.

Fig. 21 represents a case of simple inversion, bringing about the crossing tracts; the aedeagus lies uppermost.

Fig. 22 represents the curvilinear development where the terminal segments curve round to bring the aedeagus and anal papilla, still inverted, into the forwardly directed position. The crossed tracts show the direction of the curve taken.

Fig. 23 shows the anal papilla returned to the rearwardly directed position, the aedeagus retaining its forwardly directed position. The alimentary canal has caught up the genital duct, forcing it to pass over the top. This feature is brought about by the two twists, that in the vertical plane and that in the horizontal, both having the one direction shown in the diagram, namely towards the reader.





Figs. 17–19.—Illustrating the theory of correlation between the aedeagus and vagina. Fig. 17 is direct; fig. 18 is inverse. Fig. 19 illustrates the special case in the Muscoidea. The dorsal side of the aedeagus and the vagina are represented by a thickened line.

Figs. 20–23.—The digestive and genital tracts as traced from the erect terminalia (fig. 20), through the inverted hypopygium (fig. 21) and curvilinear terminalia (fig. 22) to the circumverted terminalia (fig. 23).

The anus is represented by a triangle, the dorsal side being black, and the aedeagus by a quadrangle also marked black on the dorsal side.

Fig. 22 represents the tracts seen in Syrphoidea, the curvilinear form, whilst fig. 23 represents a recovery to the rectilinear form seen in Muscoidea. Fig. 22 is to be visualised as having the tracts curving towards the reader in a manner that brings their apices nearest to him.

Obviously the same effect would be produced by the twist in figs. 21 and 22 being away from the reader. It is not known if this alternative occurs in Muscoidea, but Richards states that from his observations *Bombylius* (Asiloidea) has the twist from left to right, and *Volucella* (Syrphoidea) and *Calliphora* (Muscoidea) in the opposite direction. Feuerborn, however, draws it for *Calliphora* from left to right, and it is uncertain how much this discrepancy is to be put down to different interpretations by authors.

So far as I can make out at present, by observations and deduction, and by general references in literature, the Brachycera have the vertical twist always from left to right, and in Syrphoidea the curvilinear development takes the same direction. Only in the Nematocera does the hypopygium take the vertical twist in both directions, but I have not checked this, being guided in the opinion by literature.

A displacement of sclerites is caused through this complication throughout the Cyclorrhapha. The tracheae show the spiral twist from left to right which must ultimately bring the sternites to the position normally occupied by tergites. No authors on Muscoidea have made allowance for this, and all regard certain large sclerites of the terminalia as being tergites. A clear picture can be gained by studying the description published by Metcalf (1921, *Ann. ent. Soc. Amer.* **14** : 169–214), and augmented by the following remarks :—

It is necessary that the twist of the hypopygium be dissociated from the curving of the rest of the terminalia. First the hypopygium turns over from left to right and becomes inverted. Next the whole terminalia independently curve through a half-circle to the right so as to point the hypopygium anteriorly as seen in the Syrphid. In so doing the pleurae of these segments remain practically unaltered in size, forcing the tergites and sternites to take a general spiral twist, the sternites lying on the outer or posterior curve; the tergites being on the inner curve largely become vestigial. The hypopygium remains inverted throughout this process.

The general effect is the same as if the whole hypopygium had revolved on its axis through 360 degrees, but the evidence shows otherwise, making it necessary to amend the circumverted hypopygium theory of Feuerborn and of Richards. The latter author thought that the hypopygium turned through 180 degrees and the rest of the terminalia took two turns of 90 degrees each, but the diagram shown here indicates four segments are involved, three taking 60 degrees each of the total spiral.

III. ABDOMINAL SEGMENTATION IN DIPTERA.

Long after this paper was ready for publication (1941), Dr. Crampton kindly forwarded to me three papers giving his interpretation of the circumverted hypopygium, and this is virtually identical with the explanation given here. Dr. Crampton's first paper is in 1936, *Bull. Brooklyn ent. Soc.* **31** : 141–9; the second in 1941, *Psyche* **48** : 79–94, where he states that the first may not have carried conviction, being brief; the third is in 1942, *Guide to the insects of Connecticut*, Part **6**, Diptera, first fascicle (State Geology and Natural History Survey).

Although Dr. Crampton gives the sclerite numbering in accord with observed segments and uses the genital orifice as a convenient centre to orientate the genital complex on both sexes, this being my own method, yet we have reached quite different results from the Calliphorid type. I can offer the present view as an alternative to that of Dr. Crampton's as it seems impossible, at present, to confirm or confute either on the evidence gathered.

Snodgrass (1935, *Principles of insect morphology* : 249) states that in modern insects, the relation of definitive scleritisation to the morphological regions of the body is highly variable, and this brings about numerous anatomical inconsistencies. Dipterists treat the segments of the abdomen in various ways, coming to conflicting conclusions in their studies. Among recent authors, Feuerborn (1922, *Zool. Anz.* **55** : 49–73 and 97–111) concluded that the scutellum belongs to the metathorax, and the halteres, together with the first tergite, belong to the abdominal region, though joined to the metathorax. The first sternite and the first spiracle are in the abdominal mass. Snodgrass holds another view, namely that the thoracic mass contains the prothorax, mesothorax and appendages of the metathorax, the tergite of the metathorax being at the extreme base of the abdominal mass.

At the Entomological Society of Queensland (Minutes of the meeting April 1940, typescript), I exhibited specimens of *Neoexaireta spinigera* Wied. (STRATIOMYIIDAE), in which the scutellum articulates, moving up and down in unison with the wings. Permitting this action there is a sliding contact between the scutellum and adjacent sclerites, both front and rear. This quite unexpected feature seems to indicate that the scutellum of Diptera belongs to the metanotum as Feuerborn claimed, and if so then it becomes more evident that the first segment of the abdomen, or at least its tergite, has become part of the thoracic mass. That small depressed area just in front of the scutellum may mark the true scutellum of the mesothorax, and the scutellum of taxonomists may be the metanotum; the first tergite would then lie in the thoracic mass adjacent to the so-called scutellum, if this interpretation be correct. Possibly the true first sternite became obsolete.

Most authors count the observed segments, but there seems to be evidence of yet another segment following the ninth, only vestiges being retained. W. Hennig (1936, *Zool. Anz.* **9**), in a series of papers, has followed works including two, one by Reichardi (1929) and one by Crampton (1936), neither of which is accessible to me. Here the segment which includes the aedeagus is regarded as being the ninth and tenth segments combined, the proctiger making the eleventh.

My own observations lead me to agree with this view, but the tenth tergite appears as vestiges only in the more primitive genera in females of the Tabanoidea and Asiloidea. It is unsatisfactory, therefore, to call the ninth tergite a combined ninth and tenth tergite in the male. The tenth sternite is a vestige forming the median plate under the present interpretations, but other complications noted show that a better understanding of this region is needed.

Metcalf has taken into consideration the presumed basal segment now missing, and therefore his observed segments start with the symbol " 2 " in the place of the usual " 1 ", after which he counts only the observed segments and omits the problematical tenth segment, which is the only one taken into account by Hennig. Both authors would make the proctiger the eleventh segment, and this incorporates the cerci in the female. Cerci are never present in the male. In the present discussion only the observed tergites are counted. The median plate, which forms the tenth sternite, is retained in Syrphoidea, but is not counted as representing a segment; the tenth segment by count is the proctiger.

Fig. 24 is a diagrammatical representation of the twisting terminal segments on Cyclorrhapha, in which there are one of the four preabdominal and six postabdominal segments arranged in a linear sequence. Segment 10 is reduced to membrane surrounding the anus, but in Syrphoidea it has the remnant of lamellae in the form of flesh swellings, one flanking the anal papilla each side, similar to those of the BOMBYLIIDAE. Also in Syrphoidea the ninth tergite is formed by a small basal piece and a pair of detached flanges, the forceps. In Muscoidea the flanges alone are represented, the vestigial proctiger being adjacent to the eighth segment and flanked by the flanges of the ninth. Adjacent to the ninth tergite lies the eighth sternite which is evident because the aedeagus is inverted in Cyclorrhapha. The eighth segment, therefore, has undergone a 180 degrees rotation and the tergite is below. The seventh segment is rotated through 120 degrees but, in the Muscoidea, its sternite becomes displaced so as to overlap one of the spiracles. The sixth segment is rotated through 60 degrees. The fifth segment is erect, but its sternite bears a pair of flanges shown. The fourth segment is normal and forms the apex of the preabdomen.

The twist, as here represented, is definitely shown by Metcalf in his figure of the Syrphid curvilinear terminalia where already the aedeagus has moved forwards to lie under the eighth sternite (ninth urite in his fig.), and at its base an enlarged armature is developed. In Muscoidea the armature is reduced to a posterior spine or is absent or at most represented by a tubercle upon which the aedeagus is placed, as in some Tachinids.

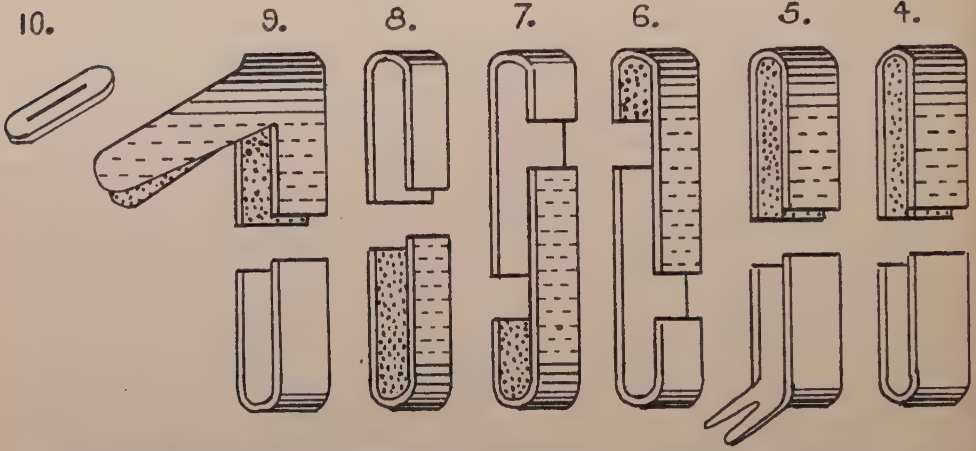


Fig. 24.—The theoretical segmentation of terminalia in Muscoidea, the tergites being marked dark and the sternites white. Flanges of the fifth and ninth segments are shown.

In Syrphoidea a phallic pouch develops in the pleura to receive the aedeagus, and this is preserved in Muscoidea as the gap lying between the tergite and sternite of the sixth segment, but the genital cavity has developed and the remnant of the sixth tergite and sternite forms the periphery of the phallic pouch.

IV. The Disposition of Terminal Sclerites in *Calliphora*.

Dr. Crampton has assumed the direction of development in terminal segmentation is directly through the Syrphid type to the Acalyptrata type and then passes to the Calyptrata type. In so doing he concludes that the seventh and eighth sternites have amalgamated in Calliphoridae. On the other hand I had assumed that the development from the Syrphid type is fanwise, the terminalia of the Acalyptrata and those of the Calyptrata developing along separate and even multiple lines with the apical spiracle retained always on the seventh segment.

Dr. Crampton has shown how the spiracles may have migrated to the eighth sternite in the Calliphorid type, but of this I am not yet convinced. Moreover I cannot see how cerci can have been retained on the male, nor can I see any homologous connection between the basi- and disti-styli forming the one pair of claspers of Orthorrhapha and the two pairs of Cyclorrhapha, which idea Dr. Crampton has recently abandoned. The solution offered below rests upon the idea that the claspers of Cyclorrhapha arise from sclerites.

The standard works of Lowne on the blowfly is referred to by all authors who study the terminalia of the Cyclorrhapha, and it seems advisable to refer to this author's illustrations as a basis for the present application of sclerite numbering.

Fig. 25 is a composition of illustrations in Lowne's *Anatomy of the blowfly*, 1870, pl. x, with the looping alimentary and genital tracts from Feuerborn 1922, and with the outline of various sclerites added. The numbering of sclerites is in conformity with the present discussion.

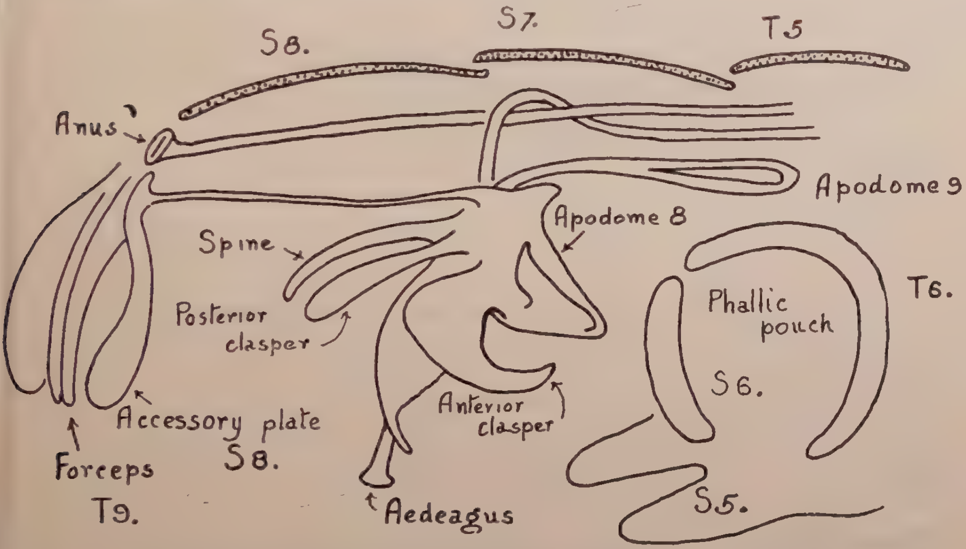


FIG. 25.—An analysis of sclerites in the terminalia of *Calliphora*. "T" marks the tergites and "S" marks the sternites, and the numbering is based upon that of fig. 24. Full explanation is given in the text.

Proctiger (membrane around the anus). This segment is practically eliminated.

Ninth tergite (T_9). Represented by flanges called "cerci" by Lowne, "stypes" by Metcalf and "lateral lobes of the tenth segment" by Snodgrass; Rhodendorf (*Faune de l'URSS*, 1937) regards them as being coxites. Taxonomists refer to them as "superior claspers" or "forceps."

Eighth sternite (S_8). This is "urite 9" of Metcalf and the tergite 9 of most authors. Frequently it bears flanges that may become detached, lying parallel with the forceps (T_9), and called the accessory plates. Taxonomists sometimes mark the sclerite as "G.S.2" (genital segment 2).

Seventh sternite (S_7). This is another dorsally placed sclerite called "sternite 8" by Metcalf, and "tergite 8" by most authors. Taxonomists may mark it as "G.S.1" (genital segment 1). Occasionally flanges are present, similar to those of the eighth sternite, but never becoming detached.

Sixth tergite (T_6). Placed askew on the upper border of the phallic pouch lies a sclerite reduced to a long transverse ridge that meets the sixth sternite only at one end, and separated by a gap at the other. This gap marks the pleural region where the phallic pouch had its origin in the curvilinear phase of its development. This tergite is marked as being the seventh by both Metcalf and Snodgrass.

Fifth tergite (T_5). This is a normal sclerite.

Fifth sternite (S_5). A pair of ventral flanges are developed on this sclerite, and together with the forceps (T_9) and accessory plates (S_8) aid in closing the genital cavity when the aedeagus is withdrawn into the phallic pouch.

Sixth sternite (S_6). A small sclerite placed askew bordering the phallic pouch, takes its rise at the base of the flanges of the fifth sternite (S_5). It is the sternite 7 of Metcalf and all those authors who believe the sixth segment to be eliminated.

Seventh tergite (T_7). The " tergite 8 " of Metcalf and the missing " sternite 8 " of Snodgrass would conform to this numbering, but as no separate sclerite is visible probably this tergite has been eliminated in *Calliphora*.

Eighth tergite (T_8). Within the genital cavity of Muscoidea, the only exposed sclerite that can be referred here is the pair of anterior claspers, one each side of the aedeagus. In *Calliphora* and allied genera, these claspers are provided with bristly hairs, suggesting their origin from a sclerite, especially as they have a musculature. In Syrphoidea this tergite is entirely missing. There is no " tergite 9 " given by Metcalf and its absence led Metcalf to doubt the origin of the sclerite he labelled " urite 9 ". The " sternite 9 " of Snodgrass is the apodeme 8, but Feuerborn marked apodeme 9 with the same symbol.

Ninth sternite (S_9). For reasons similar to those quoted under the eighth tergite, the posterior claspers may prove to be the remnant of the ninth sternite. Metcalf's " sternite 10 " is the median plate and, being on the wrong side of the aedeagus, it cannot be sternite 9. There is no " sternite 10 " according to Snodgrass.

Aedeagus. A normal feature of the Syrphoidea is the armature that lies at the base of the aedeagus and forms part of it. This armature is a secondary development sometimes found in the Orthorrhapha too, and it seems probable that the spine lying behind the aedeagus in *Calliphora* had its origin in this armature.

Apodemes. These are derived from primitive cuticular ingrowths of sclerites, and muscles are attached to them. Of the two which are involved in the present discussion, apodeme 9 operates the aedeagus and apodeme 8 is joined by ridges to the flanges of sternite 8. Feuerborn and Snodgrass identify these as sclerites by the manner of their labelling, but probably this was to mark the segment limits. The numbering given here corresponds to the segmentation with which the apodemes are now involved, not to the sequence of their origin, which may be different; and numbers here are given only to facilitate their identification.

V. The Origin of " Claspers " in Muscoidea.

It seems certain that there can be no connection between the single pair of two segmented claspers in Orthorrhapha and the two pairs of single segmented claspers in Muscoidea in so far as these organs are completely lost in Syrphoidea. The development in Muscoidea may be shown theoretically by using fig. 24, which gives a nearly lateral view of the terminal sclerites set out on a graphic plan. It is necessary to supply to this figure the aedeagus, arising between, and protruding from, the two arms of the ninth sternite. Further it is necessary to imagine this aedeagus receding so as to cut through both the ninth sternite and the eighth tergite along the median ventral line. Owing to the general reduction of the two sclerites accompanying this action, there would be left two pairs of remnants with musculature. Each pair of remnants would become minute articulating sclerites at the base of the aedeagus and, because the torque due to displacement of the musculature differs in the two segments, adaptation to control movement of these remnants would permit the now-formed claspers to swing in different directions.

Actually each anterior clasper becomes interlocked with the posterior one in a way that allows the posterior sclerite to swing laterally outwards as the anterior one is swung longitudinally rearwards, and they recover their original positions quite automatically on the relaxed fly. On display of the terminalia of a stupefied fly, this motion is seen self-impelled and the interlocking thus becomes evident.

Bristles are often present on these claspers and these mark the remnant of hairs that once covered the sclerites concerned; also they tend to disappear in the advanced genera.

BOOK NOTICE.

The caterpillars of the British Butterflies including the eggs, chrysalids and food-plants. Based upon " The Butterflies of the British Isles " by R. South. Compiled by W. J. STOKOE, edited . . . by G. H. T. STOVIN. pp. 248, 30 pls. (col.), text illust. sm. 8vo. London (F. Warne) (1944). Price 10*s*. 6*d*.

This volume is published in the " Wayside and Woodland Series " and is uniform with its parent volume, South's *Butterflies*.

It opens with a chapter by Dr. Stovin on " Instructions and Hints for rearing Butterflies in Captivity " which fills 33 pages, and is illustrated.

The body of the work, in which the immature stages are described, follows, and this part is illustrated by coloured figures, half-tone plates, and some line drawings.

The coloured plates are reproduced from original drawings by J. C. Dollman, and they have suffered much in the process.

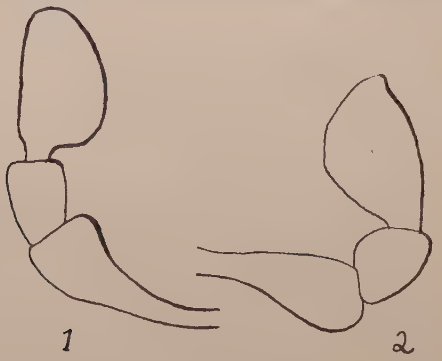
The last section of the work is that devoted to a description and illustration of the food-plants of the caterpillars of British Butterflies, listing the species which feed on them, and giving a cross reference to the full description elsewhere in the book.

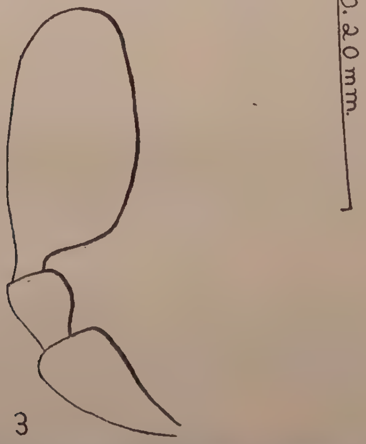
The eggs are illustrated from photomicrographs by the late A. E. Tonge and drawings by the late Horace Knight.

ON A REMARKABLE SPECIMEN OF *BYTHINUS PUNCTICOLLIS* DENNY (COL., PSELAPHIDAE)

By the Rev. E. J. Pearce, M.A., F.R.E.S.

When collecting Bythini in East Ross-shire, in the North Highland area, near Evanton, from the moss *Hylocomium splendens* B. & S., on 14.iv.1942, amongst many other specimens of *Bythinus puncticollis* Denny, I took one specimen which has subsequently given every indication of being unique, at any rate so far as British representatives of this very variable species are concerned. Further search on many occasions in the same area has failed to reveal any further specimens like it. This particular specimen, which is a female, has extremely abnormal palpi, in that the terminal joint is only about one-quarter the normal size in the case of both palpi. Mr. Harry Britten, who was kind enough to





Figs. 1 and 2.—Left and right maxillary palpus of female *Bythinus puncticollis* Denny, described in this note, showing great reduction in size of the terminal joint, also its peculiar shape.

Fig. 3.—Left maxillary palpus of "typical" female of the same species from the same locality in Ross-shire East. (All three figures are drawn to the same scale.)

examine the specimen for me, considers that it nevertheless belongs to this species, though he comments that " it is a really curious example, and of the thousands I have seen, I have never seen anything like this." Had I been able to secure further examples, perhaps of both sexes, the question would then have arisen whether it were not perhaps a peculiar race or subspecies of *puncticollis*, if not indeed a new and distinct species. As a rule, I believe it is right to say that amongst the Bythini, there is usually a much wider degree of variation amongst the males than there is amongst the females; certainly so far as my Ross-shire material is concerned I can distinguish at least two, if not three, " types " of male, if we are correct in regarding *puncticollis* Denny as a " composite " species, rather than as two closely allied species which have hitherto for a time been recognised as *puncticollis* Denny and *validus* Aubé. Mr. Britten, who has dissected a number of the males, informs me that he has tried to make two species out of all the *puncticollis* material from this area, but has eventually come to the conclusion that he is correct in regarding them all as representatives of one very variable species. This particular female therefore is all the more remarkable in differing so widely as to its palpi from all the other specimens of a much less variable sex.

As may be seen from the accompanying figure, the size of the terminal joint of the palpi (figs. 1 and 2) is greatly reduced in comparison with that of a more or less typical example (fig. 3) of the same species and sex from the same locality. So far as I can make out the two terminal joints are similar, though the right one appears to be less acuminate than the left, with its inner face considerably more rounded than in the case of the other. I have been unable to detect any other essential difference from normal limits of variation in *puncticollis*, and I now have from the Highland area alone a series of some fifty males and seventy-five females on which to base comparisons. This proportion of males to the more numerous females would hardly seem to bear out the somewhat sweeping statement made by E. C. Rye in 1866 (*British Beetles* : 236) that the males " are by far the rarest." The proportion of males to females is a subject about which I hope to say more on a future occasion; I will therefore only mention now that so far as the *puncticollis* is concerned, on only one occasion did I find an overwhelming preponderance of females—fourteen of these being taken to only one male in late August 1942, in moss near Loch Maree, Ross-shire West. I shall be very interested to hear from any coleopterists who may have specimens which in any way closely resemble the specimen described and figured in this note.

APPARENT DENSITIES OF CERTAIN AFRICAN BLOOD-SUCKING INSECTS (DIPTERA)

By F. L. Vanderplank.

(*Department of Tsetse Research, Tanganyika Territory.*)

1. Introduction.

Although there is a considerable amount of literature on the morphology and distribution of various African Tabanids, there is little information recorded as to their densities and behaviour.

The following gives a short account of catching female *Tabanus taeniola* Pal. de Beauv., *T. ditaeniatus* Macq., *T. par* Walker, *T. biguttatus* Wied., *T. africanus* Gray, *Pangonius zonatus* Walk., *P. lautissimus* Aust., *Nuceria neavei* Aust., *Dorcalaemus compactus* Aust., *D. auricomus* Aust., *D. candidolimbatus* Aust., and three unnamed species of *Haematopota* on a tethered ox during November 1940 and onwards to the end of August 1941. All these insects were caught in one hardpan area (see para. 2) near Old Shinyanga in Tanganyika Territory, primarily because they continually worried the ox which was being used for attracting *Glossina.* They were collected and recorded together with *Glossina pallidipes* Aust., and *G. swynnertoni* Aust. during each quarter-hour period throughout the day. The wet and dry bulb thermometer readings (whirling hygrometer), light intensity, black bulb temperature, evaporation rate, wind velocity, and barometric pressure were also recorded. This paper gives the numbers caught monthly and the daily mean for each species. The catches of *G. pallidipes* and *G. swynnertoni* are inserted for comparison with the others. Male Tabanids do not suck blood, so have not been included, but both sexes of *Glossina* do, and have been shown.

Unfortunately it has not been possible to have the *Haematopota* species identified and so these are given collectively under the genus. The other species have been named by comparison with specimens collected in this area by Mr. W. H. Potts, Senior Entomologist, Tsetse Research Department, and identified by the British Museum (Natural History).

2. Catching Site.

The catching site was a small hardpan about 300 by 300 yards, with riverine thickets bordering one side, and near to a small pond which is usually dry each year between the end of August and the beginning of the rains (the end of October). The catching station, under the canopy of a *Commiphora* tree, was about 100 yards from the fringes of the riverine thickets and 75 yards from the pond. Hardpan is the term given to a short-grass (up to 12 inches high) area, subjected to seasonal inundations which last only a few hours. The soil is very alkaline and, since it is deposited by flood waters, is composed of small particles and packs tightly. Rain and flood water seldom penetrate more than a foot. This area had a few evenly spaced *Commiphora* and *Lannea* trees, which are typical of hardpans.

PROC. R. ENT. SOC. LOND. (A) 19. PTS. 4–6. (JUNE 1944.)

3. METHOD OF CATCHING.

As stated in the introduction, catches were made on a stationary ox. One collector watched each side of the animal, while a third individual recorded the numbers and species caught, marked and released the *Glossina*, and read the instruments every quarter-hour. One party worked during the morning and was relieved at midday by a second party of three. The catches generally started at about 8 a.m., though a few started earlier, and stopped at 5.45 p.m., unless rain interfered with the work. The catches were made on four to twelve days each month, except in November, April and August. All the insects other than *Glossina* were placed in a killing jar and brought in to the laboratory, where they were checked against the field records by the writer, who paid daily visits and supervised the work in the field, which he always found was being carried out accurately and with considerable care.

4. OBSERVATIONS.

Table 1 gives a summary of the catches. Column 2 gives the number of quarter-hours spent catching the flies in each month. During April only one day of 29 quarter-hours ($7\frac{1}{4}$ hours) was spent in the field, because heavy rains made access to the site difficult; again during November and August only one day was spent on these observations, little time being available for this work. The rains broke during early November 1940, after the long dry season, and the rainfall for this and every other month is given in column 14. Columns 15 and 16 give the mean maximum and mean minimum temperatures for the standard station at Old Shinyanga, $2\frac{1}{2}$ miles from the catching site.

The apparent densities of the insects are best shown in Table 2, which gives the daily mean catch. The daily mean is based on 40 quarter-hour periods (10 hours—theoretically from 7.45 to 5.45 p.m. East African Standard Time, during which period these observations have shown the flies to be active). This mean represents the numbers of insects that might be expected to attack an ox during the day. *Tabanus taeniola* was active in November, but most dense during December, and was taken throughout the rains, disappearing in July after the dry season had started. Very few *T. ditaeniatus* or *T. par* were caught and these only during the early rains. One *T. africanus* Gray and three *T. biguttatus* Wied. were taken during December. Huge numbers of *Pangonius zonatus* were caught during April, the last month of heavy rainfall and a few during May, which in 1941 was unusually wet, but none was taken during the other months. A number of *P. lautissimus*, *Nuceria neavei*, *Dorcalaemus compactus*, *D. auricomus* and *D. candidolimbatus* were caught during April, and a few *N. neavei* and *D. compactus* during May, but none during the other months. The *Haematopota* species were more numerous than the TABANIDAE, but were caught only during the rains (*i.e.* from December to April). *Glossina swynnertoni* shows a rise in numbers during the rains, then a decrease during the dry season. *Glossina pallidipes* shows a large drop in numbers from November to December, then a gradual rise in density; the low mean figure of 7 flies taken during May is most probably because the observations were made at full moon (Vanderplank, 1941).

Tabanus tended to be caught during the middle hours of the day, during which hours *Haematopota* was inactive, except on days when the sun was obscured by cloud. The data available for *Pangonius* suggest maximal activity towards mid-day and on through the afternoon, slackening off in the evening.

TABLE 1.

Total monthly catches of various species of *Tabanus*, *Pangonius*, *Nuceria*, *Dorcalaemus*, *Haematopota* and *Glossina*.

Observations			*Glossina swynnertoni* (both sexes)	*Glossina pallidipes* (both sexes)	*Tabanus taeniola* (females)	*Tabanus ditaeniatus* (females)	*Tabanus par* (females)	*Pangonius zonatus* (females)	*Pangonius lautissimus* (females)	*Nuceria neavei* (females)	*Dorcalaemus candido-limbatus* and *auri-comus* (females)	*D. compactus* (females)	*Haematopota* spp. (females)	Monthly rainfall in mm.	Mean max. screen temperatures	Mean min. screen temperatures
Month 1	Days 2(*a*)	Quarter-hour periods 2(*b*)	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1940																
Nov. .	1	34	38	71	5	0	0	0	0	0	0	0	0	124·0	30·9	19·0
Dec. .	4	154	209	50	65	8	1	0	0	0	0	0	35	125·1	29·7	17·9
1941																
Jan. .	9	317	544	144	31	2	2	0	0	0	0	0	178	110·0	27·4	17·7
Feb. .	10	342	967	290	40	7	4	0	0	0	0	0	55	73·4	30·8	18·2
Mar. .	3	85	242	42	15	3	0	0	0	0	0	0	24	90·4	30·0	18·4
Apr. .	1	29	69	11	4	0	0	607	14	32	7	22	1	125·9	30·3	18·8
May .	5	184	323	32	7	0	0	92	0	3	0	9	0	92·8	29·3	18·4
June .	11	448	1,455	717	2	0	0	0	0	0	0	0	0	0·2	29·9	17·5
July .	11	396	616	642	0	0	0	0	0	0	0	0	0	Nil	29·9	15·6
Aug. .	1	40	34	64	0	0	0	0	0	0	0	0	0	15·7	29·9	17·2

TABLE 2.

Monthly mean catches per 40 quarter-hours (from data given in Table 1).

Month 1	Number of observations on which means based 2	Total *Glossina swynnertoni* 3	Total *Glossina pallidipes* 4	*Tabanus taeniola* (females) 5	*Tabanus ditaeniatus* (females) 6	*Tabanus par* (females) 7	*Pangonius zonatus* (females) 8	*Pangonius lautissimus* (females) 9	*Nuceria neavei* (females) 10	*Dorcalaemus candidolimbatus* and *auricomus* (females) 11	*Dorcalaemus compactus* (females) 12	*Haematopota* species (females) 13	Total all species 14
1940													
Nov. . .	34	45	84	6	0	0	0	0	0	0	0	0	135
Dec. . .	154	54	13	17	2	1	0	0	0	0	0	9	96
1941													
Jan. . .	317	69	18	4	1	1	0	0	0	0	0	22	115
Feb. . .	342	113	34	5	1	1	0	0	0	0	0	6	160
Mar. . .	85	114	20	7	1	0	0	0	0	0	0	11	153
Apr. . .	29	95	15	6	0	0	837	19	44	10	30	1	1,057
May . .	184	70	7	2	0	0	20	0	1	0	2	0	102
June . .	448	130	64	1	0	0	0	0	0	0	0	0	195
July . .	396	62	65	0	0	0	0	0	0	0	0	0	127
Aug. . .	40	34	64	0	0	0	0	0	0	0	0	0	98

TABLE 3.

Percentage of wild giraffe, zebra, antelopes and wart-hogs showing trypanosomes in their bloods.

	Jan.–Feb.	Mar.–Apr.	May–June	July–Aug.	Sept.–Oct.	Nov.–Dec.
Percentage infected. 1 . .	19·0	58·3	22·2	14·9	27·3	40·0
,, ,, 2 . .	11·9	37·9	26·3	18·9	9·6	31·6

Line 1 gives the percentages as published by Vanderplank, 1942; line 2 gives the original data plus an additional hundred and seventy-five wild animals shot in the Shinyanga area between September 1941 and September 1943.

5. DISCUSSION OF RESULTS.

It is interesting to note the total numbers of blood-sucking insects that may attack a single ox during any one day of each month. It is probable that a single wild antelope of similar size (for example eland, roan, greater kudu) would attract the same numbers. A herd moving about would be attacked by even greater numbers, but by less per individual.

The percentage of game showing trypanosome infections, especially the large antelopes and giraffe, varies with the season, and the writer has suggested (Vanderplank, 1942) that this might be due to relapses caused by the wet and cold conditions following heavy rain. Since that paper was written more data have been collected and these are given with the former results in Table 3; it is now suggested that the very high percentage infected during March and April may well be due *in part* to the very high density of blood-sucking insects other than *Glossina.* Although the various TABANIDAE cannot be regarded seriously as transmitters of trypanosomiasis, it has been proved that they are capable of mechanical transmission under favourable conditions, and it seems reasonable to suppose that they might be responsible for transmitting trypanosomes from one individual to another in the same herd, when the herd may be attacked and bitten by more than a thousand insects in a day, as during April. Other catches during April in a similar piece of bush nearby produced similar numbers of this *Pangonius*, so the day cited here was probably not an abnormal one for the month. Other circumstances, such as heavy rain, may lower the resistance of the animals and still be the most important factor.

6. SUMMARY.

(*a*) The paper describes the catching of *Tabanus taeniola* Pal. de Beauv., *T. ditaeniatus* Macq., *T. par* Walker, *Pangonius zonatus* Walk., *P. lautissimus* Aust., *Nuceria neavei* Aust., *Dorcalaemus compactus* Aust., *D. auricomus* Aust., *D. candidolimbatus* Aust., *Glossina swynnertoni* Aust., *G. pallidipes* Aust., and three *Haematopota* species on a stationary ox for various periods monthly from November 1940 to August 1941.

(*b*) Two tables summarise the results and give the monthly apparent densities of each species. *Tabanus* and *Haematopota* were caught in most rainy months but *Pangonius*, *Nuceria* and *Dorcalaemus* only during April and May, towards the end of the rains. *Pangonius zonatus* was taken in huge numbers during April.

(*c*) *Tabanus* was active towards mid-day, when *Haematopota* was inactive; activity of *Pangonius* was greatest at mid-day and during the afternoon.

(*d*) It is suggested that the large numbers of *Pangonius* during April may be a factor contributing to the high incidence at that period of trypanosomiasis in game.

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